

THE PROGRESS OF QUANTITATIVE METHODS IN PALAEOLOGY

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ABSTRACT. The slow progress of quantitative methods in palaeontology during the past decade threatens the survival of palaeontology. Different phenetic and cladistic methods produce different estimates of phylogenetic relations; none of these estimates is *a priori* more authoritative than others; taxonomic and phylogenetic certainty is unattainable, and probabilistic estimates of phylogeny must be accepted. Phenetic methods are well suited to estimating phylogenies from palaeontological data. Objective definitions of taxonomic entities and attribute states are essential in phylogenetic analysis. Outline analysis and landmark analysis are discussed, and the practical advantages of the former are considered to outweigh any resulting loss of homology. Techniques of outline and surface measurement and analysis are reviewed briefly. Temple's (1982a) review of ordination methods is supplemented to include standardization of entities, Projection Pursuit, Detrended Correspondence Analysis and Canonical Correspondence Analysis.

An earlier article (Temple 1982a) dealt with the use of ordination techniques in palaeontology. The present article, which may be considered a supplement to the earlier one, has a three-fold purpose:

1. to review the progress of quantitative methods in palaeontology during the last decade, and to assess the auguries for the future;
2. to consider quantitative palaeontology in the context of two current methodological debates, namely phenetics *vs* cladistics, and outlines *vs* landmarks;
3. to up-date the earlier article on ordination.

There can be no doubt that palaeontology, if it is to survive into the next century as a serious branch of science, will do so only in so far as it has transformed itself into a quantitative discipline. By its nature, palaeontology contributes primarily to the study of aspects of evolution – variation, speciation, organic diversity, the pattern of change in time – and the evidence that palaeontology brings to bear on these topics carries conviction with scientists in other disciplines only in so far as it is expressed in quantitative terms. To take two examples: polymodality of size or shape can be established only by analysis of frequencies of scores on suitable size or shape indicators; the patterns (or even the existence) of morphological change in fossil lineages or of secular change in organic diversity need to be tested against the models that can be proposed for such data, e.g. random walk with/without drift, trend-stationary process, etc. (Diggle 1990; Nelson and Plosser 1982; Mills 1990).

It must, however, be admitted that the auguries for the change in outlook by palaeontologists essential to the survival of our subject are not good. It is, after all, not many years since the Palaeontological Association gave its annual President's Award to a paper, on assemblage structure of a group of fossils, whose author stated that he had used no numerical methods whatever in his analysis. A recent compendium of palaeontological techniques sponsored by the Association (Briggs and Crowther 1989) gives only the most scanty coverage to quantitative methods. The eyes of the palaeontological world, it seems, still glaze over at the mention of eigenvectors – the word does not, for instance, appear in the index to Briggs and Crowther. It is difficult to be optimistic about the future when most of our colleagues have not yet learned even the vocabulary, let alone the practice, of quantitative palaeontology, after exposure to it during three decades.

Furthermore, the enthusiasm with which cladistic methodology has been embraced by palaeontologists during the past decade (see below) is probably to be explained by the phenomenon

noted in a wider context by Felsenstein (1988*a*, p. 113), namely that 'young, but traditionally-trained morphological systematists who tended, on the whole, to be uncomfortable with both numerical and molecular methods ... found Hennig's qualitative discussion more accessible than the numerical work which had been slowly spreading for the previous decade'.

Nevertheless, we should not despair, in spite of the disappointments of the past decade. The progress of technology in fields relevant to palaeontology (i.e. image and spatial analysis, data handling, etc.) is now so rapid, and the technology itself is so readily accessible, that notwithstanding its present doldrums palaeontology could still be revolutionized by the turn of the century – but only if we continue to provide the channels for the relevant technology to diffuse into our subject.

PHENETICS VS CLADISTICS

It seems that as far as most palaeontologists are concerned the phenetics vs cladistics debate has been resolved in favour of cladistics – whether for the reason suggested above or not. A mere handful of phenetic studies of fossil groups has been published, and even these few have been virtually ignored by other workers in the relevant fields. Phenetics is definitely not respectable in palaeontology, and word has come down from the mountain to this effect (Gould 1980, p. 110; see also Temple 1982*b*). On the other hand, a glance at any recent issue of *Palaentology* will reveal cladograms galore. In this respect, of course, our colleagues are by no means alone among taxonomists – see for instance the cladistic triumphalism of Ridley (1985, p. 81) but contrast the more cautious rejection of phenetics by the same author the following year (Ridley 1986, pp. 83–85).

In discussing the respective merits and demerits of cladistics and phenetics it is important to define the two terms accurately, and also to be clear about the purposes for which we are proposing to use these competing methodologies. As to our purposes for using cladistics or phenetics, I presume that nowadays we are not concerned primarily with classification as such, and certainly not with forcing palaeontological data into hierarchically nested Linnaean categories. Rather, we are trying to recover from our data a phylogenetic tree (not necessarily dichotomously branched) in which there is greater genetic interchange, and therefore in most cases greater phenotypic resemblance, along and within rather than between branches. Our task is therefore the same as that of the molecular biologist (Nei 1987, pp. 292 ff.; Felsenstein 1988*b*). Indeed it is simpler than his, for whereas the molecular biologist attempts to reconstruct the whole tree (including hypothetical nodes, etc.) solely on the evidence of the tips of the branches, we start with a sample of the whole tree, including taxa at or near the nodes, a circumstance that simplifies enormously the reconstruction of the tree.

When we come to define cladistics and phenetics our task is made difficult by the change that has overtaken the former word, from its broad original sense of the study of ancestor–descendant relations between taxa (Cain and Harrison 1960, p. 3; Sneath and Sokal 1973, p. 29) to its restriction to the particular form of cladistic analysis advocated by Hennig (1950, 1966); and also by the changes that Hennig's original concept has itself undergone since 1966, and by the resulting debates between different schools of cladists (Ridley 1986, pp. 86–97), as fierce and bewildering to the outsider as the theological disputes of the fourth century A.D. For present purposes I adopt the following broad definitions of cladistics and phenetics: *cladistics* reconstructs phylogeny on the basis of change in attribute states between ancestral and descendant taxa whose attribute states are specified; *phenetics* does so on the basis of distances (variously defined) between taxa whose attribute states are not necessarily specified (and may be unknown). Since change in attribute states is equivalent to one form of distance (City-block or Manhattan), the difference between the methodologies on these definitions may appear trivial. There is, however, an underlying difference in philosophy between cladistics and phenetics. Cladistics is concerned with discrete attribute states, which are assumed to be independent (Swofford and Olsen 1990, p. 415), and of which the coding either reflects the presumed evolution of the attributes or is determined *a posteriori* by some criterion (e.g. Lipscomb 1990): continuously distributed variables (including statistical means etc.) are difficult to handle by cladistic techniques and lead to results that should be treated with caution (Chappill 1989, p. 231), while some cladistic authors consider them to be inherently unsuitable for

phylogenetic reconstruction (Pimentel and Riggins 1987; Farris 1990). Phenetics, on the other hand, accepts numerical data of any type (including continuously distributed, correlated variables), and requires attribute coding to be objective and to be completed prior to analysis.

Hennig's cladistic methodology (1950, 1966) postulated that the phylogeny of a group of taxa could be reconstructed by observing the distribution of the different (usually two) states of several morphological attributes, on the assumptions: (1) that the evolutionary sequence of states in each attribute is known; (2) that each change of state happens only at a single point in the phylogeny; and (3) that the sequence of states is irreversible. There is no doubt that the rigour which Hennig's methodology has brought to phylogenetic reconstruction has been beneficial, even if it is sometimes difficult to see the intellectual wood for the impenetrable undergrowth of jargon. The logic of determining phylogenies by shared derived attributes is unassailable, and it works very well at the naive level at which it is presented for didactic purposes, e.g. the relations between a small number of hypothetical entities (say, three or four species) based on six or seven attributes in each of which ancestral and derived states can be unequivocally distinguished and all of which suggest a unique phylogeny. The trouble is, of course, that the real world is not as tidy as this. The assignment of ancestral and derived states, although sometimes fairly straightforward and objective, as for chromosomal inversions, is in other cases difficult and controversial or, as for meristic and continuously distributed morphological attributes, inappropriate and simplistic; and in these cases it is disturbing that polarity needs to be incorporated into the analysis at an early stage whereas it would arise more logically (if at all) as output from the analysis itself. Furthermore, as the number of entities and attributes is increased, so there develops a conflict, due to violations of Hennig's assumptions (2) and (3), between the phylogenies suggested by different sets of attributes. This is the problem of homoplasy, or what Felsenstein (1982, p. 381) calls Hennig's dilemma, and Friday (1987, p. 66) non-divergent change. Recent studies of homoplasy quantify the problem and demonstrate convincingly the decline in the consistency index (an inverse measure of homoplasy) with increasing numbers of entities (Archie 1989; Sanderson and Donoghue 1989, text-fig. 1): the decline appears from Sanderson and Donoghue's data to be exponential, and the consistency falls to about 30% for 70 entities. In the face of this problem the pure logic of Hennig's methodology becomes hopelessly compromised by the need to make a subjective choice between the phylogenies supported by different sets of attributes.

These problems in applying Hennig's original methodology have caused many cladists to abandon Hennig's three basic assumptions, no longer assigning ancestral and derived attribute states *a priori* (paleontologists, however, seem reluctant to take this step, except recently Adrain and Chatterton 1990), while acknowledging the extent of homoplasy and seeking the phylogeny that minimizes it. Indeed, some cladists (the so-called 'pattern' or 'transformed' cladists) no longer look upon their cladograms as having phylogenetic significance.

The distinction between cladistics and phenetics has to some extent become blurred by these changes in cladistic methodology. There appears in fact to be a continuous spectrum of phylogenetic techniques (reviewed by Felsenstein 1982; Swofford and Olsen 1990), between overtly cladistic, i.e. based on phylogenetic changes between known or hypothesized attribute states of taxa (e.g. molecular sequence data, discrete morphological data), and pure phenetic, i.e. based wholly on directly observed distances without knowledge of the states that contribute to these distances (e.g. nucleic acid hybridization and immunological comparison data). On this cladistic-phenetic spectrum the phenetic methodologies that have been used in paleontology (ordinations and dendrograms based on distances derived from attribute state lists) lie towards the phenetic end. Let us examine the two main arguments against using such methods: (1) in replacing the original data matrix by an inter-entity distance matrix, phenetic methods discard valuable information (Farris 1981, p. 22; Penny 1982); and (2) despite the claims of its proponents, phenetic methodology is not objective (Ridley 1986, pp. 39 ff.). There is a third argument based on the non-metric properties of distances, which is of relevance mainly to molecular sequence data and the concept of the molecular clock: for the opposing views see Farris (1981, 1985, 1986) and Felsenstein (1984, 1986, 1988*b*, pp. 530-532).

The first argument against phenetics is a valid but not over-riding objection to those phenetic methods that rely entirely on secondarily-derived distance data both in processing and in presentation. This is true, for instance, of dendrograms, and adds weight to other objections to the use of dendrograms, especially the subjectivity involved in flattening the cylindrical structure of the dendrogram onto the printed page for presentation (Sneath and Sokal 1973, pp. 261–264). The argument also applies to ordination techniques that depend entirely on a secondarily-derived distance matrix, i.e. the various types of multidimensional scaling. It does not, however, apply to ordination by Principal Components, which operates directly on the data matrix, and in which the original data can in principle be recovered from the transformed data that underlie the ordination. Furthermore, it is not an argument that can be used convincingly to discredit phenetics in favour of cladistics, because any loss in phenetic information must be seen in the context of the larger amount of information available to phenetic methods from their ability to handle continuously distributed attributes.

The second argument appears to be two-fold: (1) phenetic methods are sensitive to different choices of distance coefficients and clustering techniques, and (2) the subjective choices forced on the pheneticist in this way vitiate the objectivity claimed for phenetics. The validity of part (1) of the argument must be acknowledged. Recent work (Temple unpublished) shows that the concordance (as assessed, for instance, by nearest-neighbour relations) between distance matrices based on different coefficients decreases as the number of attributes increases. Furthermore, different clustering or ordinating techniques clearly produce different results even when they are operating on the same distance matrix, let alone when operating on different distance matrices. Part (2) of the argument cannot, of course, be used selectively against phenetics, since it applies with equal force to cladistics because of the need to choose between compatibility and the different forms of parsimony for resolving homoplasy: it is a valid inference from (1) only if the pheneticist or cladist accepts the need to make the subjective choice postulated by the argument. It cannot be denied that in the past many pheneticists (including the present author) and cladists have done so, either explicitly or implicitly. The valid response of the pheneticist or cladist to this dilemma, however, is to recognize that different coefficients and techniques produce different estimates of the phylogenetic relations (i.e. different tree topologies); that none of these estimates is *a priori* more authoritative than others; but that probabilities can be assigned to the different nodes and branches according to the frequencies with which they recur in different estimates, and that in this way a probabilistic estimate of the tree can be obtained.

In practice, of course, few pheneticists or cladists are likely to go to the lengths of trying all the available techniques on their data. It is, however, in the spirit of the last paragraph to present an ordination, minimal spanning tree, Wagner tree or dendrogram as no more than the result of applying a particular technique to the data, without claiming to have produced the definitive answer – and I suspect that many pheneticists and cladists do in fact have this attitude towards their results, even if it is not formally articulated. So long as the results are interpreted in this probabilistic spirit, phenetic methods – with their ability to handle meristic and continuous, correlated variables – are well suited to estimating phylogenies from palaeontological data-sets, in which significant inter-attribute correlations are known to occur (e.g. Temple and Tripp 1979, table 3; Temple 1980, table 5). In particular, since palaeontological data are a sample of the whole tree (including nodes or near-nodes), an ordination in which each entity is linked by a minimal spanning tree to its nearest neighbour (however defined) would be expected to converge progressively to the true phylogeny as the density of sampling increases. Applications of this technique (Rowell 1970; Temple and Tripp 1979; Temple 1980) might be criticized (although they do not in fact appear to have been so criticized) for implicit reliance on standardized Euclidean distance as the basis of phylogeny, but it is possible to make such ordinations overtly probabilistic by incorporating phylogenetic relations suggested by different distance measures (cf. Temple and Wu 1990, fig. 2).

We conclude from this discussion that, because of limitations of samples and techniques and because of the widespread occurrence of homoplasy, certainty is not attainable in phylogeny and taxonomy, and whatever methods we use we must be content with probabilistic statements

(Felsenstein 1985; Penny and Hendy 1986; Sneath 1986). In this context the importance of Felsenstein's conclusions cannot be too strongly emphasized: 'The adoption of a methodology that explicitly acknowledges uncertainty is a paradoxical necessity if phylogenetic inference is to be placed on a firm scientific footing' (Felsenstein 1982, p. 399).

Before leaving this topic it is worth remarking that any taxonomic/phylogenetic analysis – phenetic, cladistic or whatever – is only as good as the data on which it is based, and in particular that the objectivity of the results is limited by the objectivity of the original data. It is therefore of the utmost importance that taxonomic entities and attribute states should be defined objectively; and in both respects current palaeontological practice is lax. The most objective taxonomic entity in palaeontology is the topotype sample of a species (Temple and Tripp 1979, p. 234), and the most objective data are thus mean topotypic attribute states of species. In principle, analysis at higher taxonomic levels could be done either (1) by extending the type-concept vertically and representing any taxonomic level by the mean topotype attribute states of its type species; or (2) with some loss of objectivity, by grouping together topotype samples of designated species and calculating the relevant mean attribute states. In practice, neither of these procedures is normally followed, and many taxonomic/phylogenetic analyses in palaeontology are seriously weakened by being based on imprecisely and subjectively delimited 'genera', 'families', etc. As to attribute state definition we need only note that, if attribute states are not precisely and objectively defined, subsequent authors will be unable to repeat or extend the original observations, and not even the most rigorous analysis of such attributes could claim to be scientific.

OUTLINES VS LANDMARKS

The only valid objection that has ever been made to the use of quantitative methods in morphological palaeontology is that they are very time-consuming. This is, of course, no longer true of data-processing, but it is still true of observer-mediated data-gathering, i.e. measurement by an observer using callipers or eye-piece micrometer, and the problem is exacerbated by the need to process large samples in order to obtain statistically robust or significant results (cf. Temple 1987, p. 128). In these circumstances automated measurement is extremely desirable.

The most convenient form of automated measurement is outline analysis, of which at least four types have been used in recent years in palaeontology and related subjects. The first and most extensively used method (e.g. Kaesler and Waters 1972; Healy-Williams 1983) has been polar Fourier analysis. In this method radii are drawn from the centroid of a closed curve (usually at equal angular intervals, say of 5°), and the length of each radius is plotted as a function of the angle of rotation of the radius ($0-360^\circ$) from a zero starting direction. The resulting function is then Fourier-analysed as a sum of trigonometrical functions. Objections to this method are that it cannot be applied to complex curves with re-entrant angles, and that it depends on the identification of the centroid of the closed curve and on the definition of a zero point on the curve. The second type of outline analysis is elliptical Fourier analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982; Ferson *et al.* 1985). In this, a point travels around the closed curve at constant speed, and the x and y coordinates are separately plotted as periodic functions of time and Fourier-analysed: the curve is then approximated by superimposing a series of orthogonal ellipses (in a manner analogous to the Ptolemaic approximation to the elliptic planetary orbits by superimposing cycles of circles). The third type of outline analysis is eigenshape analysis (Lohmann 1983). Here a point travels around the closed curve at equal increments of arc, and chords are drawn to it from a zero point on the curve. The angles that successive chords make with the tangent at the zero point form a vector characterizing the curve (Zahn and Roskies 1972), and vectors from different curves form a data matrix that is analysed by Principal Components. Both elliptical Fourier analysis and eigenshape analysis are free from the objections to polar Fourier analysis noted above: both can deal with complex curves; neither makes use of the extraneous concept of the centroid; the elliptical Fourier coefficients are independent of the zero point, while Lohmann (1983) avoids the problem by an algorithm for matching the vectors from different original curves. A fourth method, perimeter-

based Fourier analysis, has been introduced recently (Foote 1989). In this, a point travels around the closed curve at equal increments of arc as in eigenshape analysis, but chords are drawn to it from the centroid rather than from the zero point, the lengths and orientations of these chords being separately Fourier analysed. This method also can deal with complex curves, but has the disadvantage of depending on the centroid and a zero point. Of these various methods, elliptical Fourier analysis is the most attractive in principle and was found to perform well by Rohlf and Archie (1984). All four methods, however, are equally liable to the fundamental objections raised recently to the use of outline analysis in morphometrics.

These objections have been cogently stated by Bookstein *et al.* (1982). Briefly, they are that outline analysis obscures homologies. (Full and Ehrlich (1986) direct this criticism specifically at eigenshape analysis and by implication absolve Fourier analysis; but see Rohlf 1986; Ehrlich and Full 1986.) Bookstein *et al.* (1982, fig. 1) illustrate their argument by two circular outlines, one with four equally spaced homologous landmarks, the other with the same landmarks unequally spaced: the two outlines are indistinguishable in their Fourier coefficients (but see below) even though they represent two very different morphologies. The example is striking, but then so is the counter-example of Read and Lestrel (1986, fig. 2) – four equally spaced landmarks linked by two very different outlines indistinguishable by landmark analysis.

There is no doubt that the concept of homology underpins the whole of comparative morphology, and that we should not set it aside lightly. It is not clear, however, that we should restrict our morphometrics entirely to homologous landmarks, as has been done in a series of elegant papers by Bookstein and his collaborators (e.g. Bookstein *et al.* 1985; Bookstein 1986). Quite a lot of useful biometric information is derived from measurements that are not strictly homologous, e.g. the maximum width of a brachiopod or of the frontal glabellar lobe of a trilobite at different growth-stages, the maximum measurable length of a bivalve mollusc without terminal umbones. Furthermore, even in the example given by Bookstein *et al.* (1982, fig. 1) the four landmarks would be likely in practice to disturb the circular outline (as indeed they do in the figure), and if the outlines were sufficiently finely digitized this disturbance would produce differences in the Fourier coefficients between the two cases. Finally, returning to our original theme, there is no doubt that, although algorithms could presumably be devised *ad hoc* to recognize homologous landmarks without observer participation, in the present state of technology outline analysis lends itself much more readily to automated measurement than does landmark analysis.

I conclude that the theoretical objections to outline analysis are not so great as to outweigh the practical advantages of automated measurement that the method offers. There are, however, some important precautions that palaeontological users of outline analysis should observe:

1. standardizing and defining accurately the viewing orientation: this may be relatively easy where the morphology itself defines a plane of symmetry or at least something approximating to such a plane, as in coccoliths, ostracodes, many bivalve molluscs, profile views of brachiopods and trilobites, etc.; it becomes more difficult when we wish to view along (rather than normal to) a plane of symmetry, as in non-profile views of brachiopods and trilobite cephalae (Temple 1972, 1970, pp. 4–6); and it becomes a non-trivial problem, that cannot be solved purely by definition, when we wish to identify the axial view of a trochospiral foraminiferan;

2. defining the reference zero point and/or (depending on the method used) zero direction on the outline;

3. ensuring that size information is not inadvertently lost (by normalizing) early in the analysis: in Fourier methods size information is carried in the coefficients of the zeroth harmonic;

4. using all the information derived from the analysis: in particular, in Fourier analysis the phase angles as well as the amplitudes carry information and should not be discarded as has happened in several palaeontological applications.

Finally, it is important not to lose sight of the fact that most fossils are three-dimensional objects, of which two-dimensional outline analysis can give only an imperfect representation. Three-dimensional measurement and analysis are clearly desirable, and could in principle be done in several different ways, including:

1. characterization by 3 orthogonal profiles;
2. direct, observer-mediated measurement of x , y and z coordinates (Lazarus 1986);
3. several different techniques of automated metrology (Jarvis 1986; Gåsvisk 1987), of which only contouring by holographic interferometry seems yet to have been applied to palaeontology (Elliott and Morris 1987).

Method (1) leads to direct parameterization in terms of 3 sets of Fourier coefficients. Methods (2) and (3) could lead to parameterization in terms of: (a) two-dimensional polynomial or Fourier series (Davis 1986, pp. 405–447) for surfaces equivalent to single-valued distances from a plane of symmetry (e.g. many ostracodes); or (b) spherical harmonics (Jacobs 1974, pp. 310–314; Bomford 1980, pp. 782–787) for surfaces equivalent to single-valued radii from a centroid (e.g. many planktonic foraminifera, acritarchs); or (c) differential geometry (Okamoto 1988), or (d) computerized surface representation methods (Tipper 1979).

ORDINATION TECHNIQUES

A major omission in the earlier article (Temple 1982*a*) was a section on the standardization of entities. The need for such standardization arises from ‘accidental’ differences between entities, particularly from differences in sample size between sites in distributional data. It is possible in some cases to remove the effects of such differences at a later stage of analysis, i.e. as the first eigenvector in Principal Components Analysis by analogy with the growth eigenvector of morphological analysis. The analogy with morphological analysis data is, however, not exact, for whereas a growth eigenvector is usually a direction of increase in all the attributes, the first eigenvector of distributional data may be determined fortuitously by the dominant species in the largest available sample; furthermore, size of an individual is an intrinsic attribute, whereas size of a fossil sample depends on extrinsic factors such as ease/difficulty of collection. For these reasons, although it is possible (indeed desirable) to retain size differences in growth analysis data, it is better for purposes of site ordination to standardize distributional data to a standard size of (say) 100. The constraint imposed on data by standardizing to constant sample size has, however, the undesirable effect of distorting the inter-attribute correlation matrix by inducing spurious negative correlations (this is the ‘closure’ problem encountered in analysis of compositional data in petrology). Ordination of the attributes (i.e. interrelations of taxa) in distributional data should therefore be based on unstandardized data.

Three ordination techniques have become available since the earlier article was prepared, namely, Projection Pursuit, Detrended Correspondence Analysis, and Canonical Correspondence Analysis.

Projection Pursuit (Friedman 1987; Jones and Sibson 1987) is designed to seek out projections (i.e. combinations of attributes) that maximize the inhomogeneity of the data. Projection Pursuit does not yet appear to have been used on palaeontological data, but would be expected to be useful for testing whether morphological variation (size and/or shape) was continuous or discontinuous. As yet, however, Projection Pursuit can apparently handle only fairly small data matrices.

Detrended Correspondence Analysis (Hill and Gauch 1980) is a technique designed to remove an artefact (the ‘horseshoe’ effect) that may appear in ordinations of phyto-sociological data. When vegetation is sampled along an environmental gradient the gradually changing floral composition along the gradient would be expected to show up as a linear seriation of the sites along the first ordination axis, with sites at the environmental extremes furthest apart in the ordination; instead, there is a curvilinear relationship between site scores on the first two (or more) axes, so that the extreme sites are not at the extremes of the ordination. Digby and Kempton (1987, pp. 93–97 – see especially tables 3.2, 3.11, and figs 3.14–3.15) give a very clear account of the phenomenon, which is attributable to underestimation of the distances between sites at opposite environmental extremes and ultimately to a special, quasi-diagonal, form of the data matrix. Palaeontological data matrices of this form arise in biostratigraphy (e.g. Rickards 1976, table 1), and ordinations of such matrices might therefore be expected to lead to horseshoes. This is true, for instance, of the MDSCAL ordination of two pollen sequences by Gordon and Birks (1974, p. 237, fig. 7), and in this case

detrending would probably make more perspicuous the stratigraphical correlation established by Gordon and Birks between the two sequences. The possibility therefore arises of correlating stratigraphical sequences by the scores of the individual horizons on the first axis of a Detrended Correspondence Analysis.

Canonical Correspondence Analysis (ter Braak 1986) is a technique that produces a simultaneous three-fold ordination of *sites* at each of which have been observed the occurrences or abundances of various *taxa* and the values of various (environmental) *variables*: a detrending option is available. This powerful technique clearly has considerable potential in palaeoecological studies, but no applications appear to have been published so far.

Finally, it may be useful to list some relevant general publications that have appeared in the last decade. There are good summaries of ordination techniques by Gordon (1981), Dunn and Everitt (1982), ter Braak (1987), and Digby and Kempton (1987), as well as in the new edition of Davis's invaluable book (1986). Several examples of palaeontological ordination are given in Temple (1987).

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